Apparent zoogeographical dispersal patterns in two avian families

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INTRODUCTION

Darlington (1957), after studying the zoogeography of the various vertebrate classes, presented a hypothesis for a general pattern of vertebrate evolution and dispersal. This assumed that there had been a common area of origin and evolution of successive dominant groups in the main part of the Old World tropics (Ethiopian and Oriental) and a spread into smaller and less favourable areas, with successive replacement of earlier groups by more recent groups of species which, by their plasticity and vigour, would tend to be dominant. Owing to the restrictions imposed by the configuration of land-surface this spread would tend to be channelled along three routes, one southwards into southern Africa and Madagascar, another south-east through the East Indies into Australasia and the Pacific, and a third via Eurasia into North America and thence to South America. As each group radiated from the centre of origin, it would tend to replace earlier groups, so that, although some overlap would occur, the earliest groups would tend to persist only at the extremities of the routes of dispersal, while the more recent groups would be most apparent at the centre of origin. Such a pattern would, of course, be modified by subsidiary factors affecting dispersal.

Darlington experienced difficulty in attempting to trace the evidence of evolution and dispersal underlying the present pattern of bird distribution, and commented that "the dispersal of dominant birds has probably often been so rapid and also so complex as to be beyond analysis." He considered however that the present distribution was the result of the movement of birds over something like the existing land pattern, being relatively recent in terms of geological history.

Some of the examples which Darlington mentioned suggested that a dispersal of the type which he described had taken place. In the Caprimulgiformes he found a pattern of threefold radiation—an early one which left small isolate families in Central America, Australia, and the Oriental Region, then the radiation of the family Caprimulgidae and that of the genus *Caprimulgus*. The fact that the last two resulted in a cosmopolitan distribution prevented him from drawing any conclusions regarding the centre of origin. He also listed examples of discontinuous distribution with apparently closely related species or genera occurring on different continents, citing *Spizaetus* (Accipitridae) found from eastern Asia to New Guinea, and again in tropical America; *Dendrocygna viduata* (Anatinae) in Africa and South America; *Porphyrula* (Rallidae) in Africa and Central and South America; *Ciccaba* (Strigidae) in Africa and Central America; the two similar genera *Lophostrix* and *Jubula* (Strigidae), one in Central America and one in Africa; and *Picumnus* (Picidae) in the Oriental region and South America. These latter examples do not however offer evidence of the type of dispersal envisaged unless one can show that their present distribution is related to the presence of later replacement groups.

In recent studies of certain avian families, involving the examination of data on plumage, morphology and behaviour, in order to clarify relationships of various species, it was found that there were taxa within the families which appeared to show evidence of the type of dispersal and replacement suggested by Darlington for other vertebrates. It seemed possible that a failure to find more widespread evidence of this pattern in avian distribution might be due to an expectation that this type of dispersal and replacement would be apparent at familial level, whereas it in fact appears to be more evident in lower taxa.

In a study of this kind some attempt must be made to separate evidence of major dispersive movements and the affinities of the species involved from the multitude of minor factors which will tend to modify the main trends. Such conclusions as are made will necessarily have a highly subjective basis and due allowance must be made for this. Ultimately the accuracy of the observations probably depends on the extent to which the species relationships within the families can be deduced and interpreted.

In the present study, evidence which was thought to indicate this dispersal pattern was found in the typical doves, subfamily Columbinae of the Columbidae, and in the waxbills, Estrildidae.

In this paper the following zoogeographical regions are recognised; Ethiopian, extending into Arabia; Oriental, from India to Celebes, Sula, and Lesser Sundas, and including the Philippines, Pacific islands to the east of them; Australasia, including New Guinea, Moluccas, and New Zealand, and islands south and east of the Moluccas; Palaearctic, the region between the Mediterranean and India being a part of this and also a link between the Ethiopian and Oriental regions; Central America, including areas immediately north and south of the Caribbean, and the Caribbean islands; North America, and South America. Where the distribution of any taxon extends into more than one such region the regions are hyphenated; *e.g.* Oriental-Australasian.

THE PATTERN OF DISPERSAL

From a consideration of the groups studied it was found possible to construct an ideal pattern of this type of dispersal as it would appear in lower avian taxa. The pattern is due (in part) to the fact that species tend to become more divergently specialised according to the length of their period of existence, and that taxonomic arrangements are influenced by such specialised differentiation.

The oldest group of species would show an interrupted distribution towards the ends of the routes of dispersal (*i.e.* in some or all of the following regions—South Africa and Madagascar, South America, Australasia). They would tend to show extremes of adaptation and to occur as well-marked species with a tendency to limited and possibly discontinuous distribution. The differences which had evolved between species would result in their taxonomic arrangement in small and often monotypic genera, or in some cases separation into different higher taxonomic categories. In areas where competition with later dominant groups, or other species with similar ecological requirements, did not occur, considerable adaptive radiation would be likely to have taken place.

The middle group or groups of species would tend to have a wider and more continuous distribution, but would be likely to be absent from extreme or isolated areas. Genera would be relatively few and the entire group might be regarded as a single genus. Species would tend to be stable and well defined, and speciation would be likely to have occurred to an extent where, in different areas, similar species would have evolved which replaced one another geographically. Adaptive radiation would be less apparent and the species would be more likely to resemble one another. They would probably tend to be relatively less specialised in their needs, but nevertheless adapted for definite ecological niches.

The recent groups of species would tend to have a more limited distribution near the centre of origin, with a few species showing greater dispersal. Speciation would tend to be less well-defined, and it might be difficult to be certain of specific and subspecific separation. Major extensions of range, and hybridisation where sympatry occurred, would be likely. Species would tend to lack very specialised ecological requirements and to be more likely to adapt themselves to environmental changes.

The division into three major categories here is largely a matter of convenience of concept, the number of successive groups being likely to vary from one family to another.

THE APPARENT EVIDENCE OF DISPERSAL

1. COLUMBINAE.

Within this subfamily three main subdivisions can be recognised—a large bronzewing group, a medium-sized *Columba* group and a small *Streptopelia* group. The pattern of taxonomic arrangement in these groups can be summarised as follows:—

Bronzewings.

Oriental-Australasian regions.	1 genus of 2 species.
Australasian region.	3 genera of 1 species, 5 genera of 2 species, 1 genus of 3 species, 1 genus of 18 species on islands.
Ethiopian region.	2 genera of 1 species, 1 genus of 4 species.
Americas.	4 genera of 1 species, 3 genera of 2 species, 1 genus each of 3, 4, and 5 species, 1 genus of 15 species and 3 of 1 species on and around Caribbean islands.

Columba.

Nearly cosmopolitan. 1 genus of 52 species, divided into four subgenera with 1 species, 3 species, 4 species and 44 species. The last subgenus has been divided into 5 species groups, comprising 15 subgroups.

Streptopelia.

Ethiopian-Oriental-Palaearctic regions. 1 genus of 15 species.

(a) *Bronzewings.*

The earliest of the above groups would appear to be the bronzewings. This term has been used here is reference to a group of species centred around those having iridescent patches or spots on the wing-coverts. When a study was made of certain plumage characters of pigeons it was concluded (Harrison 1960) that there was evidence of a large bronzewing group of species in the Columbinae. This group had been recognised by Salvadori (1893) who treated them as a family, the Peristeridae, but they were not separated by Peters (1937). The tendency within the group is for a loss of the distinctive markings, and the iridescence on the wing-coverts is most extensive in the single species, *Chalcophaps indica*, occurring in the Oriental region. In the Australasian region it has given rise to a second sibling species. In addition to the iridescent wing colouring *Chalcophaps* also shows the chestnut colour on the primaries and the pale head pattern that appear to be recurring characters within this group.

In Australia apart from the four fruit pigeons of the genus *Ptilinopus*, and *Columba norfolcensis*, all other species are considered to belong to this group. They comprise the following genera—*Petrophassa* (2 species), *Phaps* (2 species), *Ocyphaps* (1 species), *Lophophaps* (2 species), *Geophaps* (2 species), *Histriophaps* (1 species), *Geopelia* (3 species), and *Leucosarcia* (1 species). Outside Australia *Geopelia striata* is found through the East Indies to Malaya, and another genus *Henicophaps* (2 species) occurs in New Guinea.

These species show the type of extreme differentiation which results in a taxonomic arrangement with numerous small or monotypic genera. There is considerable size variation and some morphological variation with a marked tendency towards adaptation for terrestrialism. Iridescence on the wing-coverts is most marked in *Phaps*, and is present in ten Australian species, but within the group it shows a tendency to disappear and *Petrophassa* shows only a tiny concealed patch on one feather, while in *Leucosarcia* and *Geopelia* it is absent. The *Geopelia* species show a barred plumage pattern which is apparent in some degree in other genera such as *Geophaps* and *Lophophaps* and is apparent otherwise in the juvenile plumage. Varying degrees of chestnut colouring are present on the inner web of primary feathers, this being another character which appears to show a gradual loss. In one species of *Petrophassa* and some races of *Geopelia striata* this area of the flight feathers lacks pigment and the chestnut areas are replaced by white. Several species show the development of crests by elongation of the feathers of the crown.

The eighteen species of the ground dove, genus *Gallicolumba*, which occur over a wide area of Australasia and the Pacific share morphological and plumage similarities with the bronzewings and are here considered to have radiated from the bronzewing group. The large number of species is due to speciation within an island distribution. Both these and the Australian species appear to fill the niche occupied elsewhere by medium-sized gamebirds. In view of the extreme divergence and specialisation shown by various genera in this area, it seems possible that the Oriental-Pacific genus *Macropygia* may also form a part of the bronzewing group. Species in the latter genus have long tails and in some cases barred plumage.

The subfamily Gourinae should also be mentioned here. It consists of the now extinct monotypic *Microgoura* with a specialised bill and crest, and three *Goura* species. All occur in the New Guinea area. The *Goura* species are huge birds with flat lacy crests and purple patches on the blue-grey wings and they are ground doves. The purple area on the wing-coverts might be homologous with the iridescence apparent in bronzewing species, and the crest could be foreshadowed in some of the crested Australian species. The extreme divergence shown by these species suggests that they may be relicts of an earlier dispersal but in many respects they appear to be more closely linked with the bronzewings than with other doves.

The African bronzewings comprise only five species, all of them relatively small birds. They are ground-feeders, but do not show marked specialisation for this. This apparent lack of adaptive radiation might be due to competition with successive dove groups and with the medium-sized ground-feeding gamebirds which are present in numbers in Africa. The African genera are *Turtur* (4 species), *Tympanistria* (1 species), *Oena* (1 species). Most occupy arid or semi-arid country. *Turtur brehmeri*, a larger and more brightly coloured species of forest areas, was regarded at one time as a member of a monotypic genus *Chalcopelia*. *Oena capensis* is tiny, long-tailed and tends to be nomadic. All these species have either small iridescent spots on some wing-feathers, or black markings replacing these, and all show chestnut colouring on the inner webs of the primaries.

In Central and South America the situation is again more complex. There is an assemblage of species of small ground doves most of which show iridescent, or more frequently black, patches or spots on the wing-coverts. Peters (1937) recognised seven genera—*Claravis* (3 species), *Columbina* (1 species), *Uropelia* (1 species), *Scardafella* (2 species), *Metriopelia* (4 species), *Oxypelia* (1 species), *Columbigallina* (5 species). This arrangement was further subdivided by Hellmayr and Conover (1942) to produce ten genera, but subsequently this has been reduced by Goodwin (1959a) to five. It illustrates a similar taxonomic pattern to that which occurs in the Australian doves, many genera being recognised, each containing only a few species. Black and iridescent wing markings occur in all but four species, and two of the remaining species of *Scardafella* show a convergent resemblance to an Australian species, *Geopelia striata*, in plumage pattern, shape and size. Only five species show chestnut pigment on the webs of the flight feathers. As in the Australian and African species there appears to be a tendency for a loss of the common signal patterns: these species show some degree of adaptation. Species of the genus *Metriopelia* appear to be adapted for an existence at high altitudes and one species has become a hole-nester.

As in the Australasian and Pacific areas, so also in the South and Central American areas there are genera of larger doves which may have been derived from the ancestral forms of this group. *Zenaida* (Goodwin 1958), which comprises *Zenaidura* (2 species), *Zenaida* (2 species), and *Nesopelia* (1 species) of Peters (1937) is a group of larger doves with a distribution extending into North America. These species show dark

spots on the wing-coverts, and in *Nesopelia galapagoensis* there is a heavily-spotted pattern comparable with that of the smaller American bronzewing species. The extinct *Ectopistes migratorius* appears to have had a close affinity with these species, and the whole group may represent adaptive radiation from the bronzewing stock.

In addition to these there is a group of quail-doves in Central America which Peters (1937) considered were close to *Gallicolumba*. Goodwin (1958) has pointed out that this may be convergent resemblance and that this group appears to be closely related to *Zenaida*. The group comprises *Osculatia* (1 species), *Oreopelia* (15 species), *Geotrygon* (1 species) and *Starnoenas* (1 species). Goodwin (1958) has combined most of these in the genus *Geotrygon*, retaining *Starnoenas* as a related species sufficiently distinct to justify a possible monotypic genus. The large number of species in the genus *Oreopelia* of Peters (*op. cit.*) may be compared with that of *Gallicolumba* in the Pacific with its 18 species. In both groups distribution over a large number of islands has resulted in speciation and in both cases ground doves of convergent form and plumage have been produced.

(b) *Columba.*

The group of species which appears to have replaced the bronzewings over a wide central area is that which is taxonomically regarded as a single genus *Columba*. This arrangement in a single unit is an indication of the relative similarity to one another shown by these species. The genus has a wide and continuous distribution over Africa, Asia, and the Palaearctic, extending from Japan southwards into the Pacific and East Indies with one species just reaching Australia. In addition there is another group occupying South and Central America and the southern part of North America. The genus is not wholly uniform and indivisable. Goodwin (1959b), in a review of its taxonomy, recognised four subgenera. Three of these are minor groups probably representing either divergence in isolation or the relict forms of a minor dispersal wave—*Nesoenas* (1 species) of Mauritius, *Turturoena* (3 species) of Ethiopia and *Oenoenas* (4 species) of Central and South America. Within the remaining subgenus Goodwin recognised five species groups, and within these fifteen subgroups, mostly comprising from three to five species, although a few were represented by a single species.

These doves are, for the most part, medium-sized to large birds which do not show extreme differences of structure and habit. They exhibit some adaptation to particular habitats, and have produced tree-dwelling and rock-dwelling forms, and forms which replace each other altitudinally. In most cases specific distinctions are clearly defined. Goodwin considered that within the genus the greatest amount of adaptive radiation had occurred in the Palaearctic and Ethiopian regions. The American species require special consideration. They are absent from much of North America and do not show any obvious evidence of a Eurasian link in their distribution. This discontinuity might, however, be due to changes in general distribution due to Pleistocene glaciation, the effects of which extended considerably further south in North America than was the case in Eurasia. The present species may subsequently have arisen by diver-

gence and speciation within the Central and South American regions. Studies such as those of Cumley and Irwin (1944) and Johnston (1962) which show that these species are more closely related to each other than to any Eurasian species would appear to confirm such an origin but would not justify claims that this group was independent of the *Columba* complex unless it could be shown that they were in fact more closely linked with some other dove genus, or that the discontinuity was as great as those separating other groups from *Columba*.

(c) *Streptopelia*.

The relatively small genus *Streptopelia* comprising fifteen species, appears to show the type of distribution and other characters suggested for a recent species group. The distribution is an Ethiopian-Oriental one with a pair of sibling species, *S. turtur* and *S. orientalis* extending as migrants over the Palaearctic region. These latter species show differences that would be regarded as of subspecific importance only, were it not that their ranges overlap and they show ecological separation where they meet. Another two species, *S. chinensis* and *S. bitorquata* extend into the East Indies.

This genus has fewer species but these tend to have wide distributions. Of the patterned-back *turtur* types, two migrate northwards into Europe and Siberia, while a third, *S. lugens*, occupies North Africa except for the Sahara. Of the patterned-neck species one, *S. senegalensis*, extends over all Africa and through Arabia to India while the other, *S. chinensis*, extends from India and China into western East Indies. The remaining ten species form a plain-back, ring-neck group with *S. torquata* in the East Indies, *S. tranquebarica* in India and China, *S. decaocto* from Asia Minor to China, *S. picturata* in Madagascar and islands off East Africa, and the remaining six species form a group in Africa, closely resembling one another and many of them sympatric in distribution.

In addition to the close resemblance of *S. turtur* and *S. orientalis*, the two species *S. decaocto* and *S. roseogrisea* form another pair which are taxonomically difficult to separate. Plumage differences are in any case slight in these birds, but although there are distinct differences of voice the two appear to hybridise if they meet. Hybridisation within the whole genus appears to occur with relative ease and frequency under captive conditions. Although there is some size difference, especially where more than one species is present in an area, the species are, as a whole, uniform in appearance and behaviour and do not appear to show any extreme of variation and adaptation.

The most striking feature of this group is its apparent relative adaptability, especially to conditions created by man. There is one form that has been domesticated for so long that its origin has been in doubt. It appears to have been in existence since the period of the Roman Empire. This is the so-called Barbary Dove, at one time given the specific name of *S. risoria*. It has been linked by some authorities with *S. decaocto*, but the variant plumage is not a useful character and the voice is that of *S. roseogrisea*. Peters (1937), when stating the distribution of *S chinensis*, refers to introduction into Mauritius, Hawaii, Celebes, Moluccas, and islands in the Flores Sea. *S. picturata* is said to have been introduced into

Mauritius, Reunion, and the Seychelles, although Peters (*op. cit.*) seems to imply that this may have been part of a natural extension of distribution. *S. chinensis* has also been introduced and established itself successfully, though usually in areas modified by man, in Australia, New Zealand, and parts of California. *S. senegalensis* has also established itself in Australia. The most striking change in distribution has, however, been shown by *S. decaocto*. Apparently without help from man, though always in conjunction with human settlement and partly dependent on human activity, this species has spread in a relatively short time to colonise Europe. It is suggested that the genus is one which, compared with the bronzewing and *Columba* groups, is still relatively plastic and is actively adapting itself to its environment.

(d) *Other dove groups.*

The other major group outside the Columbinae, the fruit pigeons (Treroninae of Peters) has not been studied here, but according to D. Goodwin (pers. comm.) it appears to show evidence of the evolution of two successive major groups; a *Ptilinopus-Ducula* group showing more extreme adaptation and variation and with a wide distribution through the Oriental-Australasian-Pacific regions, with an isolated group on and around Madagascar; and a *Treron* group with an Ethiopian-Oriental distribution. The latter group is more uniform in appearance with fewer species recognised, but many subspecies.

GENERAL COMMENTS (Columbinae)

It must be assumed that when later evolutionary groups arise it is probable that they have been derived from some part of an earlier group within the same area. Presumably both *Columba* and *Streptopelia* would have a bronzewing ancestral form. Since *Streptopelia* will have had less time to diverge from this than will *Columba*, this might account for the apparent affinity, revealed in Sibley's (1960) study of egg-white protein, between the former genus and some of the genera considered here to belong to the bronzewings. The position of *Aplopelia* is of interest in this respect. This African species has a discontinuous montane and island distribution suggesting a relatively early origin and the sum of its characters place it somewhere between the *Turtur* bronzewings and *Streptopelia*. It has been suggested that it is a *Streptopelia* adapted for a *Turtur* niche. The present study suggests that this would be atypical for *Streptopelia* as a whole and that *Aplopelia* might represent an early offshoot from the same stock that gave rise to the later *Streptopelia* or represent a direct linking form.

In the comments on *Streptopelia* it has been implied that adaptation to co-existence with man may represent the environmental adaptation of a "recent" species. It is, however, recognised that other species from older groups have increased their range under similar circumstances. *Geopelia striata* has been successfully introduced into Madagascar and other islands off East Africa, St. Helena and Hawaii, and possibly its presence in Celebes and Amboina may be due to introduction (Peters 1937). Similarly *Columba livia* has been carried into every part of the world by man.

(*to be continued*)